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ORIGINAL ARTICLE

The importance of sexual, asexual and mixed ramet clusters in production of descendant ramets in populations of *Solidago* ×*niederederi* (*Asteraceae*)

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Abstract

In this study, we focused on the potential production of descendant ramets in sexual, asexual, and mixed ramet clusters of *Solidago* ×*niederederi* Khek (*Asteraceae*), a natural hybrid between the North American *S. canadensis* and the European *S. virgaurea*. We selected eight populations of the hybrid occurring in southern Poland. The ANOVA results proved the significant effect of cluster type and population on the number of descendant ramets in sexual, asexual, and mixed ramet clusters. The post-hoc Tukey test showed that the number of descendant ramets in sexual and mixed ramet clusters differs significantly ($p < 0.001$). The number of descendant ramets was positively correlated with the number of maternal ramets in sexual, asexual, and mixed ramet clusters, reaching the coefficient values of 0.78, 0.64, and 0.82, respectively. Moreover, the number of descendant ramets was positively correlated with the height of maternal ramets in mixed ramet clusters, reaching the coefficient value of 0.25. The post-hoc Tukey test revealed the significant differences between the height of ramets originating from sexual and asexual ramet clusters ($p < 0.001$). Our results complemented the current state of knowledge and brought evidence that the number of descendant ramets might be influenced by a type of ramet cluster.

Keywords Alien species · Clonal growth · Generative and vegetative ramets · Hybrid · *Solidago*

Introduction

The presence of two modes of reproduction (sexual and asexual) plays a major role in naturalization and invasion of alien plant species (Pyšek 1997; Pyšek and Richardson 2007). The long-term studies on various aspects of sexual (e.g., seed production and dispersion, soil seed bank, seed germination, seedling survival) and asexual propagation (e.g., production of vegetative offspring, persistence of connections between the ramets, lateral spread) in introduced plants are strongly recommended to determine their naturalization and invasion status in floras (Pyšek et al. 2004; Richardson and Pyšek 2012). The successful naturalization and invasion by sexual and asexual reproduction have been well documented in many clonal plants such as *Eichhornia crassipes* (Mart.) Solms. (Barrett 1980a, b; Chu et al. 2006; Buchanan 2015), *Spartina anglica* C. E. Hubb. (Mullins and Marks 1987; Thompson 1991; Hacker et al. 2001), *Reynoutria japonica* Houtt. (Hollingsworth and Bailey 2000; Forman and Kesseli 2003; Krajsek and Koce 2015), and *Robinia pseudoacacia* L. (Jung et al. 2009; Masaka and Yamada 2009; Castro-Díez et al. 2014). According to Milbau and Stout (2008), clonal growth is one of the most important factors associated with the naturalization of alien plants.

Despite the growing interest in the role of clonality in naturalization and invasion of plant species, the current state of knowledge is still insufficient, especially in the case of natural hybrids between alien and native plant species which should be treated as alien species (Pyšek et al. 2004). It is commonly known that in many plant hybrids the sexual reproduction is prevented by their sterility (Stace 1975) and therefore the clonal growth (if occurs) is the only reassurance for the

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persistence in the wild. Nevertheless, the investigations on intraspecific differences in the production of descendant ramets between the sexual (generative) ramet clusters (all ramets with the flowers), asexual (vegetative) ramet clusters (all ramets with no flowers), and mixed ramet clusters (some ramets with and other without the flowers) are rather neglected not only in hybrids between alien and native plant species.

In this study, we focused on the potential production of descendant ramets in sexual, asexual, and mixed ramet clusters of *Solidago ×niederederi* Khek (*Asteraceae*), a natural hybrid between the North American *S. canadensis* L. and the European *S. virgaurea* L. (Pliszko 2015; Pliszko and Zalewska-Gałosz 2016). We aimed to test the hypotheses that (i) the number of descendant ramets in the mixed ramet clusters is higher than in the sexual and asexual ramet clusters, and (ii) the number of descendant ramets in particular types of ramet clusters (sexual, asexual, and mixed) is positively correlated with the number and the height of the maternal ramets. In addition, we tested the height difference between the sexual and asexual ramets of the hybrid.

Materials and methods

Study species

The hybrid origin of *Solidago ×niederederi* was successfully confirmed by morphological, molecular, and phytochemical methods (Karpavičienė and Radušienė 2016; Pliszko and Zalewska-Gałosz 2016; Radušienė et al. 2018); however, its ecology is poorly recognized (Pliszko and Kostrakiewicz-Gierałt 2017, 2018). It has been naturalized in several countries in Europe, including Austria, Poland, Lithuania, and Latvia (Pliszko and Kostrakiewicz-Gierałt 2017; Jaźwa et al. 2018 and literature cited therein). It occurs in anthropogenic habitats such as abandoned fields, disused quarries, roadside slopes, railway embankments, tree plantations, and arable fields with grass-legume mixtures, being associated with its parental species (Pliszko and Kostrakiewicz-Gierałt 2017 and literature cited therein). It spreads by wind-dispersed fruits (cypselae); however, the seed-set in the hybrid is limited by reduced pollen viability (Migdałek et al. 2014; Karpavičienė and Radušienė 2016).

Solidago ×niederederi, a perennial polycyclic plant, forms clonal clusters of shoots (ramets) similar to those found in *S. virgaurea*. However, the number of shoots in clonal clusters of the hybrid is usually higher than in *S. virgaurea* (Pliszko 2013). Moreover, as currently known, the hybrid has no ability to form long rhizomes which are found in *S. canadensis* (Pliszko and Kostrakiewicz-Gierałt 2017). Interestingly, based on field observations, the clonal clusters of shoots of the hybrid can be divided into three types, namely sexual ramet clusters (all shoots with the capitula), asexual ramet clusters (all shoots with no capitula), and mixed ramet clusters (some shoots with and other without the capitula). Generally, the asexual shoots of *S. ×niederederi* are characterized by the condensed leaves on the apex forming pseudo-rosettes (Gudžinskas and Žalneravičius 2016) and they are usually shorter than sexual shoots.

All the ramets in clonal clusters of the hybrid arise from the resting buds located on the caudices (Pliszko and Kostrakiewicz-Gierałt 2017). During the growing season, some of the resting buds develop into shoots (asexual or sexual) or small leaf rosettes at the base of the shoots, whilst others stay untransformed. Furthermore, leaf rosettes of the hybrid can also sprout into new shoots from one season to another, similarly to leaf rosettes of *S. virgaurea*. According to Pliszko and Kostrakiewicz-Gierałt (2017), the resting buds located on caudices are essential for *S. ×niederederi* persistence and ramet production and the hybrid produces more sexual shoots (generative ramets) than asexual ones (vegetative ramets) regardless of the type of habitat and the size of the clone.

Field studies

The number of descendant ramets (stem buds and young leaf rosettes located on the caudices) in *Solidago ×niederederi* was counted in plants from eight populations occurring in southern Poland, in September and October 2017 (Table 1). For each population, 20 clusters of ramets (clones) were randomly sampled, including 10 sexual and 10 mixed clusters, respectively. The clusters of asexual ramets of the hybrid were sampled only from four populations, namely in Kraków, Wolbrom, Januszowice, and Palcza (Table 1), due to their rare occurrence in the wild. Altogether, 250 ramets from 80 sexual ramet clusters, 540 ramets from 80 mixed ramet clusters, and 31 ramets from 16 asexual ramet clusters were sampled. The area of sampling for each population was 0.5 ha. The clusters of ramets were dug out using a trowel and washed with water to remove the soil from the caudices. Next, the maternal ramets were separated manually from the clusters counting the descendant ramets (resting buds and young leaf rosettes) on their caudices. Moreover, the height of sexual and asexual ramets was measured with a self-retracting metal tape measure. The hybrid was identified in the field using morphological characters provided by Nilsson (1976) and Gudžinskas and Žalneravičius (2016). None of the examined clusters of ramets of the hybrid had long rhizomes.

Statistical analyses

The data were log10 transformed to meet the normal distribution prior to further statistical analyses. To test the differences

Table 1 Origin of *Solidago ×niedererderi* populations selected for the study

No	Locality	GPS coordinates and altitude	Habitat type	Date of descendant ramet counting
1	Lanckorona near Izdebnik	49°51.540'N/19°43.917'E; 358 m a.s.l.	abandoned field	24 Sep 2017
2	Kraków (Mydlniki)	50°05.291'N/19°50.603'E; 234 m a.s.l.	disused limestone quarry	28 Sep 2017
3	Czajowice	50°11.172'N/19°48.434'E; 435 m a.s.l.	abandoned field	28 Sep 2017
4	near Książ Wielki	50°26.134'N/20°07.875'E; 262 m a.s.l.	tree plantation	30 Sep 2017
5	near Wolbrom	50°22.144'N/19°44.715'E; 395 m a.s.l.	abandoned field	1 Oct 2017
6	near Januszowice	50°15.315'N/20°02.585'E; 288 m a.s.l.	abandoned field	2 Oct 2017
7	Palcza	49°48.552'N/19°45.135'E; 512 m a.s.l.	abandoned field	7 Oct 2017
8	Zadroże	50°17.455'N/19°46.131'E; 288 m a.s.l.	abandoned field	8 Oct 2017

between (i) the number of maternal ramets produced by sexual, mixed and asexual ramet clusters and (ii) the number of descendant ramets produced by sexual, mixed and asexual ramet clusters, (iii) the number of descendant ramets produced by one sexual ramet in sexual and mixed ramet clusters, (iv) the number of descendant ramets produced by one asexual ramet in asexual and mixed ramet clusters, (v) the height of ramets in sexual and asexual clusters, (vi) the height of sexual ramets in sexual and mixed ramet clusters, and (vii) the height of asexual ramets in asexual and mixed ramet clusters the ANOVA for factorial designs (with population as random factor and cluster type as fixed factor) followed by post-hoc Tukey HSD test was applied. Moreover, the relation between (i) the number of maternal and descendant ramets in sexual, asexual, and mixed ramet clusters, (ii) the number of maternal sexual ramets and descendant ramets in mixed ramet clusters, (iii) the number of maternal asexual ramets and descendant ramets in mixed ramet clusters, (iv) the height of maternal ramets and the number of descendant ramets in sexual, asexual, and mixed ramet clusters, (v) the height of maternal sexual ramets and descendant ramets in mixed ramet clusters, and (vi) the height of maternal asexual ramets and descendant ramets in mixed ramet clusters were tested using a correlation coefficient at the level of $p \leq 0.05$. The statistical analyses were performed using a STATISTICA 13 software package.

Results

Production of descendant ramets

The mean number of maternal ramets in sexual, asexual, and mixed ramet clusters of *Solidago ×niedererderi* was 3.1, 1.8, and 6.8, respectively. The statistical analysis revealed the significant effect of cluster type and population on the number of maternal ramets in sexual, asexual, and mixed ramet clusters (Table 2). The post-hoc Tukey test revealed the significant differences among sexual and mixed ramet clusters ($p < 0.001$). Moreover, it showed the significant differences between the populations from Wolbrom and Czajowice ($p < 0.001$).

The mean number of descendant ramets produced by one sexual ramet cluster was lower than the mean number of descendant ramets produced by one mixed ramet cluster and higher than the mean number of descendant ramets produced by one asexual ramet cluster, reaching the values of 18.6, 38.6, and 12.9, respectively. The statistical analysis revealed the significant effect of cluster type on the number of descendant ramets in sexual, asexual, and mixed ramet clusters (Table 3). The post-hoc Tukey test showed that the number of descendant ramets in sexual and mixed ramet clusters differs significantly ($p < 0.001$).

Table 2 The ANOVA results for factorial designs of the effect of cluster type and population on the number of maternal ramets in sexual, asexual, and mixed ramet clusters

	Effect (F/R)	Sum of squares	Degrees of freedom	Mean square	*F*-value	*p* value
Intercept	Fixed	17.54	1	17.54	133.95	$p < 0.001$
Cluster	Fixed	5.47	2	2.73	47.51	$p < 0.001$
Population	Random	1.26	7	0.18	3.44	0.04
Cluster*Population	Random	0.52	10	0.05	0.65	0.77
Error		12.48	156	0.08		

Table 3 The ANOVA results for factorial designs of the effect of cluster type and population on the number of descendant ramets in sexual, asexual, and mixed ramet clusters

	Effect (F/R)	Sum of squares	Degrees of freedom	Mean square	*F*-value	*p* value
Intercept	Fixed	114.55	1	114.55	1093.75	$p < 0.001$
Cluster	Fixed	5.30	2	2.65	46.89	$p < 0.001$
Population	Random	0.65	7	0.09	2.24	0.11
Cluster*Population	Random	0.41	10	0.04	0.34	0.97
Error		18.40	156	0.12		

The mean number of descendant ramets produced by one sexual ramet in sexual ramet clusters was lower than the mean number of descendant ramets produced by one sexual ramet in mixed ramet clusters, reaching the values of 5.94 and 6.73, respectively. The statistical analysis revealed the significant influence of interaction of cluster type and population on the number of descendant ramets (Table 4). The post-hoc Tukey test proved the significant differences between the mixed ramet clusters from the population of Czajowice and all generative clusters ($p < 0.01$) and all mixed clusters ($p < 0.001$). Moreover, the remarkable differences were observed between the mixed ramet clusters from Palcza and sexual ramet clusters from Kraków, Książ Wielki, Lanckorona ($p < 0.001$) and Januszowice ($p < 0.01$), as well as mixed ramet clusters from Kraków ($p < 0.001$). Also, the mixed ramet clusters from Lanckorona differed significantly from sexual ramet clusters from Kraków and Książ Wielki ($p < 0.001$), as well as mixed ramet clusters from Kraków ($p < 0.001$). Simultaneously, the post-hoc Tukey test showed a lack of differences among the sexual ramet clusters from all populations.

The mean number of descendant ramets produced by one asexual ramet in asexual ramet clusters was significantly higher than the mean number of descendant ramets produced by one asexual ramet in mixed ramet clusters, reaching the values of 7.22 and 5.32, respectively. The statistical analysis revealed the significant influence of interaction of cluster type and population on the number of descendant ramets (Table 5). The post-hoc Tukey test showed the significant differences between the mixed ramet clusters from Czajowice and other populations ($p < 0.001$), as well as asexual ramet clusters from Wolbrom and Palcza ($p < 0.001$).

The number of descendant ramets was positively correlated with the number of maternal ramets in all three types of ramet clusters, reaching the coefficient values of 0.82 (for mixed ramet clusters), 0.78 (for sexual ramet clusters), and 0.64 (for asexual ramet clusters). Moreover, this positive correlation was also revealed for sexual and asexual ramets of the mixed ramet clusters treated separately, reaching the coefficient values of 0.85 and 0.86, respectively. The number of descendant ramets was positively correlated with the height of maternal ramets in mixed ramet clusters, reaching the coefficient value of 0.25. Considering sexual and asexual ramets of the mixed ramet clusters separately, the number of descendant ramets was also positively correlated with the height of maternal ramets, reaching the coefficient values of 0.18 and 0.15, respectively. In the case of sexual and asexual ramet clusters, the correlation between the number of descendant ramets and the height of maternal ramets was statistically insignificant, reaching the coefficient values of 0.06 and 0.15, respectively.

The height of sexual and asexual ramets

The sexual ramets of *Solidago ×niederederi* in sexual ramet clusters were significantly taller than the asexual ramets in asexual ramet clusters, reaching the average height of 102.9 cm and 20.3 cm, respectively. The statistical analysis revealed the significant effect of cluster type on the height of

Table 4 The ANOVA results for factorial designs of the effect of cluster type and population on the number of descendant ramets produced by one sexual ramet in sexual and mixed ramet clusters

	Effect (F/R)	Sum of squares	Degrees of freedom	Mean square	*F*-value	*p* value
Intercept	Fixed	278.47	1	278.47	524.89	$p < 0.001$
Cluster	Fixed	0.61	1	0.61	1.46	0.27
Population	Random	4.46	8	0.56	1.24	0.41
Cluster*Population	Random	2.67	6	0.45	8.81	$p < 0.001$
Error		27.99	553	0.05		

Table 5 The ANOVA results for factorial designs of the effect of cluster type and population on the number of descendant ramets produced by one asexual ramet in asexual and mixed ramet clusters

	Effect (F/R)	Sum of squares	Degrees of freedom	Mean square	*F*-value	*p* value
Intercept	Fixed	35.03	1	35.03	78.39	$p < 0.001$
Cluster	Fixed	0.003	1	0.003	0.02	0.91
Population	Random	6.32	6	1.05	2.12	0.32
Cluster*Population	Random	0.84	3	0.28	4.88	$p < 0.001$
Error		13.76	241	0.05		

ramets (Table 6). The post-hoc Tukey test showed the significant differences between the height of ramets originating from sexual and asexual ramet clusters ($p < 0.001$).

Moreover, the sexual ramets in sexual ramet clusters were significantly taller than the sexual ramets in mixed ramet clusters, reaching the average height of 102.9 cm and 94.1 cm, respectively. The statistical analysis revealed the significant influence of interaction of cluster type and population on ramet height (Table 7). The post-hoc Tukey test proved that mixed ramet clusters from Czajowice differed significantly from mixed ramet clusters from Książ Wielki ($p < 0.001$) and sexual ramet clusters from Lanckorona and Czajowice ($p < 0.001$). In contrast, the asexual ramets in asexual ramet clusters were significantly shorter than the asexual ramets in mixed ramet clusters, reaching the average height of 20.3 and 35.2, respectively. The statistical analysis revealed the significant influence of cluster type on ramet height (Table 8). The post-hoc Tukey test showed the significant differences in asexual ramet height between the asexual and mixed ramet clusters ($p < 0.001$).

Discussion

Our hypothesis that the number of descendant ramets in the mixed ramet clusters is higher than in the sexual and asexual ramet clusters of *Solidago* ×*niederederi* cannot be fully accepted due to significant differences between sexual and mixed ramet clusters solely. The hypothesis that the number of descendant ramets in particular types of ramet clusters (sexual, asexual, and mixed) is positively correlated with the number and the height of the maternal ramets can be partly accepted because of the lack of correlation between the number of descendant ramets and the height of maternal ramets in sexual and asexual ramet clusters. The greatest number of descendant ramets in mixed ramet clusters can be explained by the fact that the number of maternal ramets in the mixed ramet clusters was the highest. The pattern of asexual reproduction indicating that the larger clones (with the higher number of ramets) produce more offspring is well recognized (Cain and Damman 1997). Moreover, the greatest production of descendant ramets per one maternal ramet noticed in asexual ramet clusters of *S.* ×*niederederi* corresponds to the results of other investigations on clonal plant species. For example, Falińska (1986, 1995) and Kostrakiewicz (2007) argued that the vegetative individuals in a pre-reproductive phase considerably (even severalfold) increase the number of aboveground units, while in the later developmental stages (generative, senile) the effectiveness of vegetative propagation gradually decreases. According to Stuefer (1998 and literature cited therein), the totipotent interconnected ramets of clonal plants can specialize functionally in the performance of the limited number of tasks such as the uptake of resources, carbohydrate storage, vegetative spread, and sexual reproduction. The sexual ramets of *S.* ×*niederederi* not only provide the genetic variation and contribute to a long-distance spread by wind-dispersed fruits but they are also involved in vegetative reproduction, showing a positive correlation between the number of maternal and descendant ramets in both sexual and mixed ramet clusters. In this connection, the formation of sexual, asexual, and mixed ramet clusters promotes the naturalization and further spread of the hybrid.

Table 6 The ANOVA results for factorial designs of the effect of cluster type and population on the height of sexual ramets in sexual ramet clusters and asexual ramets in asexual clusters

	Effect (F/R)	Sum of squares	Degrees of freedom	Mean square	*F*-value	*p* value
Intercept	Fixed	70.09	1	70.09	588.53	$p < 0.001$
Cluster	Fixed	4.42	1	4.42	107.31	$p < 0.001$
Population	Random	1.54	7	0.22	21.89	0.87
Cluster*Population	Random	0.11	3	0.04	0.65	0.59
Error		15.30	269	0.06		

Table 7 The ANOVA results for factorial designs of the effect of cluster type and population on the height of sexual ramets in sexual and mixed ramet clusters

	Effect (F/R)	Sum of squares	Degrees of freedom	Mean square	*F*-value	*p* value
Intercept	Fixed	703.62	1	703.62	20675.34	$p < 0.001$
Cluster	Fixed	0.08	1	0.08	2.95	0.21
Population	Random	0.12	3	0.04	1.07	0.53
Cluster*Population	Random	0.06	2	0.03	3.26	$p \leq 0.05$
Error		2.12	225	0.009		

It is not easy to explain the lack of correlation between the height of maternal ramets and the number of descendant ramets in sexual and asexual ramet clusters, whereas it was confirmed in the mixed ramet clusters. However, it should be pointed out that the mean number of maternal ramets in sexual and asexual ramet clusters was significantly lower than in the mixed ramet clusters and a total number of asexual ramet clusters sampled for the study was very low. This might be the reason why the results of correlation for mixed ramet clusters and total sample were the same. Nevertheless, the positive correlation between the height of maternal ramets and the number of descendant ramets was previously noticed in *S. altissima* L. (Cain 1990b), while the positive correlation between the height of maternal ramets and the number of new rhizomes was found in *S. gigantea* Aiton (Botta-Dukát 2016). Moreover, Hartnett (1990) and Schmid et al. (1995) noticed the positive relationship between the size of *S. canadensis* genets and the mass of rhizomes allowing the clonal growth. The positive relationship between the size of maternal ramets and clonal progenies was also observed in other species such as *Trientalis europaea* L. (Piqueras and Klimeš 1998). Simultaneously, it is worth mentioning that the rate of ramet production affects their local density and substantial changes in living conditions, which in turn limits ramet recruitment (Olejniczak 2003).

In this study, the stem buds and young leaf rosettes located on the caudices of the hybrid were treated as potential descendant ramets; however, their transformation into new shoots was not investigated. Although it was recently evidenced that the number of ramets in *S. ×niederederi* can effectively increase from one season to another (Pliszko and Kostrakiewicz-Gierałt 2017), the lifespan of ramets and the longevity of clones of the hybrid remain unknown. Interestingly, *S. virgaurea*, in which the clonal clusters of ramets resemble those found in the hybrid, has perennial ramets and low vegetative mobility (Tamm et al. 2002). Given this, further investigations on the clonal growth of *S. ×niederederi* are needed.

In the established and invading populations of *S. canadensis*, the production of synflorescences depended on shoot size and appeared in all shoots which attained a height of 70 cm (Bradbury 1981). Similarly, Cain (1990b) evidenced that in *S. altissima* the percentage of flowering ramets increased steadily with ramet height. The height difference between the sexual and asexual shoots was also clearly noticeable in *S. ×niederederi* populations. Moreover, in the mixed ramet clusters of the hybrid, the sexual ramets were shorter than those in the sexual ramet clusters, whereas the asexual ramets were taller than those in the asexual ramet clusters. The occurrence of such differences between the types of ramet clusters in relation to age of the clones and environmental conditions should be intensively studied in the future to justify their ecological importance. It is also worth mentioning that Szymura and Szymura (2013) found positive correlations between the height of *S. gigantea* and percentage of organic matter and total nitrate in the soil, as well as between inflorescence length of *S. gigantea* and total nitrate in the soil.

The hitherto studies on *Solidago* populations suggested that the production of descendant ramets can be influenced by the local environmental conditions, e.g. stage of secondary succession (Hartnett and Bazzaz 1985), distance to the closest

Table 8 The ANOVA results for factorial designs of the effect of cluster type and population on the height of asexual ramets in asexual and mixed ramet clusters

	Effect (F/R)	Sum of squares	Degrees of freedom	Mean square	*F*-value	*p* value
Intercept	Fixed	326.17	1	326.17	1387.04	$p < 0.001$
Cluster	Fixed	0.79	1	0.80	1.09	0.37
Population	Random	2.50	6	0.42	0.34	0.87
Cluster*Population	Random	2.68	3	0.89	8.83	$p < 0.001$
Error		27.49	272	0.10		

neighbour (Meyer and Schmid 1999), character of adjacent species (Cain 1990a), and herbivore activity (Cain et al. 1991). We proved that the differences in the production of descendant ramets by one sexual/asexual ramet of *S.* ×*niederederi* might be a simultaneous effect of cluster type and population. In conclusion, our results complemented the current state of knowledge and brought evidence that the number of descendant ramets might be influenced by a type of ramet cluster and that in the mixed ramet clusters the number of descendant ramets is higher than in the sexual and asexual ramet clusters and it depends on the number and the height of maternal ramets.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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